

**FACTORS AFFECTING POPULATION GROWTH***Notes***I. Density Dependent and Density Independent Mortality Factors**

- A. L. O. Howard and W. F. Fiske (1911) were the first to base a concept of population regulation on functional relationships. They proposed the terms "catastrophic" mortality factors and "facultative" mortality factors.
1. Catastrophic Mortality Factors: factors destroying a constant proportion of a population regardless of the organisms being acted upon.
  2. Facultative Mortality Factors: factors destroying a percentage of a population which increases in destruction with increases in the population. They respond to population changes in host or prey density.
- B. H. S. Smith (1935) rephrased the terms into "density independent" and "density dependent" mortality factors.
1. Density Independent (Catastrophic) Mortality Factors: those mortality factors that are a function of the non-living (abiotic) physical components of the environment
  2. Density Dependent (Facultative) Mortality Factors: those mortality factors that are a function of biotic agents in the environment
    - a. Intraspecific competition: competition among a species
    - b. Interspecific competition: competition between 2 species
- C. Density dependent mortality factors
1. Reciprocal density dependent mortality: that mortality inflicted on a population by a biotic mortality factor whose own numbers are changed as a consequence (i.e., *Vedalia* beetle on cottony cushion scale). The different types of reciprocal density dependent mortality are:
    - a. Direct density dependence
      - overcompensating ( $b > 1.0$ ) UNSTABLE
      - perfect ( $b = 1.0$ )
      - undercompensating ( $b < 1.0$ ) STABLE
    - b. Inverse density dependence
    - c. Delayed density dependence (time lags)
  2. Nonreciprocal density dependent mortality: that mortality inflicted on a population by a biotic mortality factor whose own numbers are not changed as a consequence (i.e., solitary wasps competing for a limited number of nest hole sites).

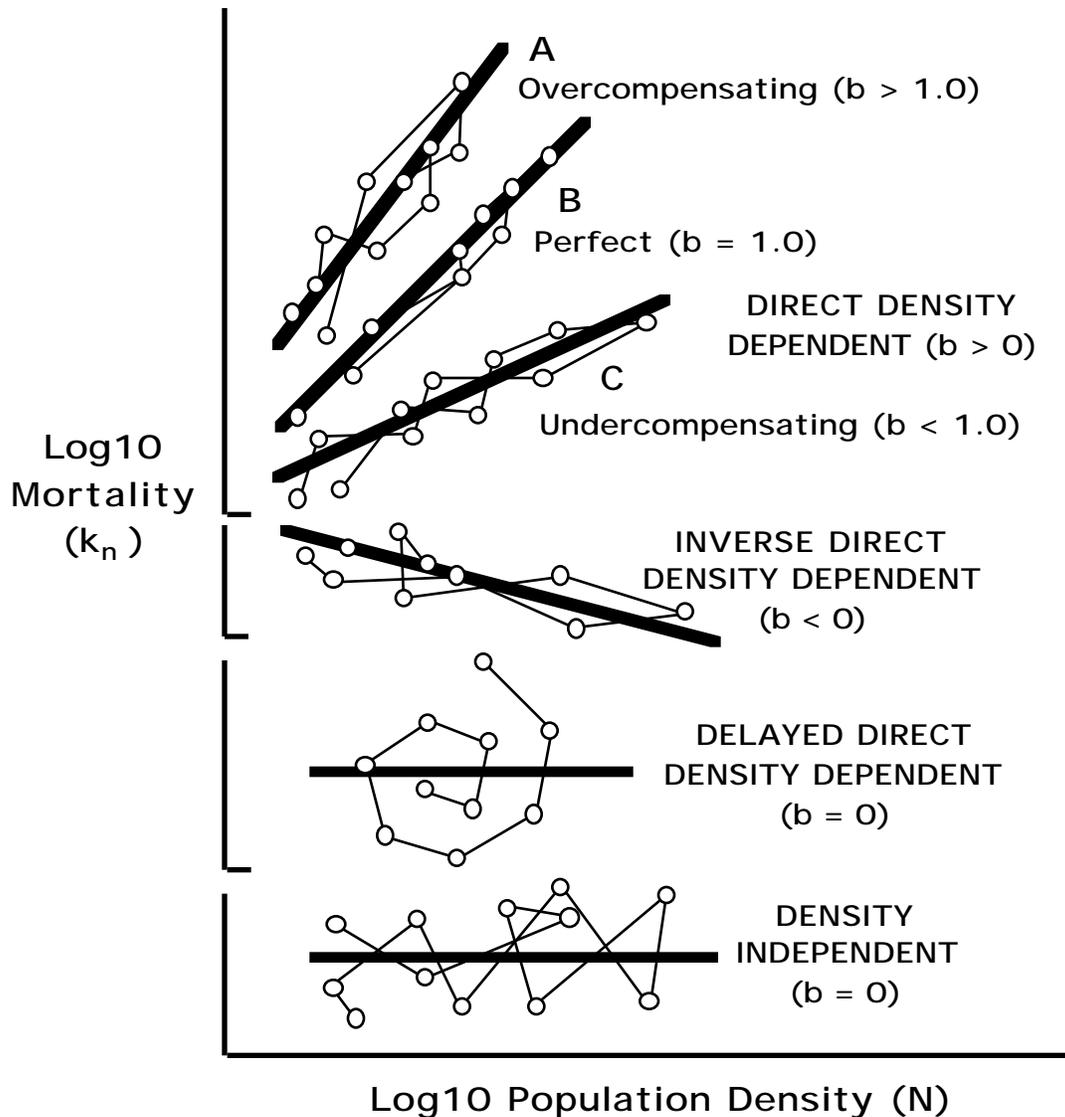


Fig. 10.1. The relationships between  $\log_{10}$  mortality ( $k_n$ ) and  $\log_{10}$  density, illustrating various types of density-dependent relationships. (A) Overcompensating direct density dependence; (B) perfect direct density dependence; (C) undercompensating direct density dependence; (D) inverse density dependence; (E) delayed density dependence; and (F) density-independent (Figure modified from Varley *et al.* 1974, see publication for more details).

## Notes

### II. Logistic Growth Theory

- A. Verhulst (1838) developed the logistic growth equation for analyzing the growth of populations. However, his work was ignored and eventually forgotten.
- B. Pearl and Reed (1920) developed the logistic growth equation independently and initiated the field of quantitative population ecology. Logistic growth equation later referred to as the "Verhulst - Pearl" growth equation.
- C. Logistic growth: the combination of the tendency for populations of organisms to grow in numbers according to a geometric progression, and the tendency for the environment to inhibit the attainment of excessively high densities by such growing populations.

Notes

- D. The logistic growth equation is a mathematical representation of Malthus' idea of population growth and environmental resistance.
- E. Concept of Chapman (1931)
  - 1. Chapman viewed population size determination as a balance between "biotic potential" and "environmental resistance".
  - 2. "biotic potential": the maximum, inherent rate of reproduction (considered fixed only under a given set of conditions).
  - 3. "environmental resistance": the totality of factors tending to limit the actual growth of populations.
- F. "Equilibrium Density": characteristic level of abundance of populations in nature. Concept that developed from the basic premises of the Verhulst-Pearl logistic theory and Chapman's theories. It is theorized that densities of natural populations (though tending to fluctuate in time) attain characteristic levels of abundance, rather than increasing without limit or decreasing to extinction.

**III. Logistic Growth Model (Equation)**

- A. See information box on next page.
- B. See parameter variation and resulting numbers in table below.
- C. Problems with logistic growth equations:
  - 1. Most populations are too complex to offer situations where the model can be tested adequately;
  - 2. The value of "r" varies with temperature and is not constant;
  - 3. The model is unsuitable to describe growth where:
    - a. The rate of increase is normally high;
    - b. The longevity of the different age classes is long relative to the time periods considered;
    - c. Environmental resistance through competition is not a linear function of density; and
    - d. The carrying capacity, "K", can be reduced by excessive feeding in real life situations.

Density (N) of a population at Time (T) as affected by changes in the intrinsic rate of increase (r) and the carrying capacity (K).

Time (Hrs)	r <sup>1</sup>				K <sup>2</sup>			
	0.01	0.10	0.20	200	338	500	2000	
0	<b>3.84</b>	3.84	3.84	3.84	<b>3.84</b>	3.84	3.84	
50	<b>6.28</b>	213.10	336.67	6.25	<b>6.28</b>	6.30	6.32	
100	<b>10.24</b>	336.67	337.99	10.11	<b>10.24</b>	10.30	10.40	
150	<b>16.55</b>	337.99	338.00	16.13	<b>16.55</b>	16.76	17.09	
200	<b>26.45</b>	338.00	338.00	25.27	<b>26.45</b>	27.04	28.03	
250	<b>41.51</b>	338.00	338.00	38.51	<b>41.51</b>	43.08	45.80	
300	<b>63.39</b>	338.00	338.00	56.45	<b>63.39</b>	67.27	74.40	
1000	<b>336.67</b>	338.00	338.00	199.53	<b>336.67</b>	497.08	1953.88	
1500	<b>338.00</b>	338.00	338.00	200.00	<b>338.00</b>	499.98	1999.68	

<sup>1</sup>K = 338 adults/jar of wheat

<sup>2</sup>r = 0.01 population increase/hr

**POPULATION GROWTH**

According to the "Malthusian Principle", the rate of growth expressed in mathematical terms is:

$$dN/dt = rN \tag{1}$$

where the first term ( $dN/dt$ ) indicates a change in the population density  $N$  for every change in time  $t$ ; and  $r$  is the intrinsic rate of population increase. If the population density at any time  $t$  is desired, then the integral of Equation 1 must be used:

$$N_t = N_o e^{rt} \tag{2}$$

where  $N_t$  is the population density at time  $t$  (hours, days, years, etc.);  $N_o$  is the initial population density;  $e$  is the base of the natural logarithms ( $= 2.71828$ );  $r$  is the intrinsic rate of increase; and  $t$  is the amount of time of population increase.

Unfortunately, the exponential growth curve did not adequately describe how populations increase in reality. Under natural conditions, food supplies always have an upper limit. Malthus did not consider the fact that food supplies would not continue to increase (even at an arithmetic rate). Later, Pearl and Reed (1920) published a paper on the growth of human populations and utilized the logistic equation developed by Verhulst in 1838 (Pearl and Verhulst developed their ideas independently). The logistic function describes certain growth processes which are bounded. The exponential growth process is an unbounded process because it will grow without limit if unchecked. In logistic growth, the initial growth is very rapid and the rate of growth increases. As the population approaches its natural limit ( $K$ ), the rate of growth decreases. The equation takes the form:

$$dN/dt = rN [(K - N)/K] \tag{3}$$

where  $r$  = the intrinsic rate of increase;  $N$  = the population density; and  $K$  = the carrying capacity of the environment. To calculate the population density at time  $t$ , one must use the integral of Equation 3 which is:

$$N_t = K / (1 + b e^{-rt}) \tag{4}$$

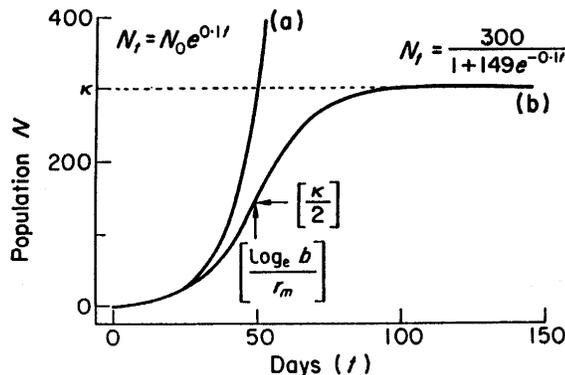
where  $N_t$  = the population density at time  $t$ ;  $K$  = the carrying capacity of the environment;  $r$  = the intrinsic rate of increase;  $t$  = the amount of time the population has been growing; and  $b$  is an arbitrary constant which may be calculated from:

$$b = (K - N_o) / N_o \tag{5}$$

or

$$\ln b = t'/r \tag{6}$$

where  $N_o$  = initial population density;  $r$  = intrinsic rate of increase;  $K$  = carrying capacity; and  $t'$  = the time at which the population is increasing at the fastest rate (when  $N_t$  is equal to one half  $K$ ).



## C. Problems with logistic growth equations:

1. Most populations are too complex to offer situations where the model can be tested adequately;
2. The value of "r" varies with temperature and is not constant;
3. The model is unsuitable to describe growth where:
  - a. the rate of increase is normally high;
  - b. the longevity of the different age classes is long relative to the time periods considered;
  - c. environmental resistance through competition is not a linear function of density; and
  - d. the carrying capacity, "K", can be reduced by excessive feeding in real life situations.

**IV. McArthur and Wilson (1967) proposed "r" and "K" selection.**

- A. Density independent and density dependent mortality factors and events differ significantly in their effect on natural selection and on populations.
- B. Highly variable environments: in these, catastrophic mass mortality often has relatively little to do with the genotypes and phenotypes of organisms concerned or with the size of the populations.
- C. Highly stable environments: in these, much mortality is highly directed and the conditions favor individuals better able to cope with high population densities and strong competition.
- D. Organisms in highly uncommon environments seldom deplete their resources to levels as low as organisms living under more common environments. Thus in uncommon habitats competition is usually less.
- E. When competition is low the best reproductive strategy is to put maximal amounts of matter and energy into reproduction and to produce as many total progeny as possible in the shortest time possible = "r selection"
- F. When competition is high the best strategy is to put more energy into competition and maintenance and to produce offspring with more substantial competitive abilities = "K selection".
- G. When dealing with "r" and "K" selection you should remember that:
  1. No organism is completely "r" or "K" selected (not a black and white situation);
  2. One should think of a "r" > X > "K" selection continuum; and
  3. An organism's position along the continuum varies with the particular environment it is in at a given instant of time
- H. Those species thought of as "r" strategists are found more in temperate regions vs. "K" strategists which are found in the more climatically stable tropics.
- I. Example: Chrysomelid beetle, *Chrysolina quadrigemina*, occurs in California and British Columbia (Canada). In British Columbia the beetles lay more eggs than those in California due to latitudinal differences. Selection is working to increase "r" in Canada.

QUESTIONS
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1. What are density independent and density dependent mortality factors? What terms did L. O. Howard and W. F. Fiske use to describe these mortality factors?
2. Graphically display the various forms of density dependent mortality factors.
3. What is logistic growth? What factors prevents its continuation in any given environment? What general term is given for these factors?
4. Where do the "r" and "K" terms originate in "r" and "K" selection?
5. How does the concept of "r" and "K" selection relate to biological control? What type (r vs. K selected) of insects are most easily controlled by biological control? What type are insect pests usually?

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**READING ASSIGNMENT:**

- Chapter 18: pp. 367–398, **Van Driesche, R. G. and T. S. Bellows, Jr. 1996.** Biological control. Chapman and Hall, New York. 539 pp.